

The biology, functional morphology and taxonomic status of *Fluviolanatus subtorta* (Bivalvia: Trapeziidae), a heteromyarian bivalve possessing "zooxanthellae".

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ABSTRACT

The biology and functional morphology of *Fluviolanatus subtorta* is described. The species occupies coastal lagoons along the eastern coast of Australia and is widespread, in estuaries, throughout the continent. The shell is heteromyarian in form with a reduced anterior slope and a long, thin, internal ligament overlain by fused periostracum. The hinge plate possesses no hinge teeth and there is no byssal notch. The thin shell comprises two layers: an outer crossed lamellar layer and an inner complex crossed lamellar layer. Ventral mantle fusion involves the inner folds only and the siphons are short with few papillae. The large ctenidia comprise both lamellae and the ciliation is of Type C (1) (Atkins 1937). The labial palps are small. The style sac and mid gut are initially conjoined but soon separate. The stomach is of Type V (Purchon, 1960) and adapted for dealing with large amounts of fine particles. The life style is discussed.

Hitherto, *Fluviolanatus* has been located in the Mytilacea. This study shows that this species is a typical eulamellibranch and after comparison with heteromyarian representatives of known heterodont families it is concluded that the genus should be more correctly located in the Trapeziidae (Arcticacea), its closest relative being the coral-associated nestler *Coralliophaga*.

Major interest centres around the greatly enlarged inner and outer folds of the ventral mantle margin. These possess large numbers of what appear to be vegetative algal cells. It has proven to be impossible to obtain further specimens for more detailed study but the cells are some $8\ \mu$ in diameter and have all the characteristics of "zooxanthellae" (e.g. *Symbiodinium microadriaticum*) typically symbionts of, among others, hermatypic scleractinian corals, giant clams of the genera *Tridacna* and *Hippopus* and the cockle *Corculum*. The possible nature of this symbiosis between *Fluviolanatus* and its "zooxanthellae" is discussed. More research is called for on this unusual bivalve.

INTRODUCTION

Fluviolanatus subtorta is widely distributed in New South Wales, Australia, occurring in rivers and coastal lagoons, byssally attached to matted algae. It has hitherto been assigned to the Mytilacea Rafinesque (sub family Modiolinae Keen 1958) (Iredale, 1924), subsequent investigators uncritically accepting this taxonomic placing (Soot-Ryen, 1969).

During a visit to The Australian Museum, Sydney, in 1972, *Fluviolanatus* was initially brought to my attention by Dr. Winston Ponder and a short time for investigation was sufficient only to determine that the genus was indeed wrongly located with the mytilids. During a further visit to Sydney in 1979, an opportunity was taken to re-examine *Fluviolanatus* in more detail.

The evolution of the heteromyarian form characteristically results in a loss of dentition, so often a clue to phylogenetic affinity within the Bivalvia. Conversely, similarities are enhanced because of convergent adaptations to the same life style. Thus, despite important specific evidence to the contrary, Purchon and Brown (1969) linked together the Mytilacea and Driessenacea. A similar situation has hitherto existed with *Fluviolanatus*; its form superficially suggesting a link with the Mytilacea. This investigation seeks primarily, on the basis of features other than shell characters, to ascribe *Fluviolanatus* to its correct taxonomic position. But it also illustrates very interesting, hitherto unsuspected aspects of the biology of this unusual and enigmatic bivalve.

MATERIALS AND METHODS

Specimens of *Fluviolanatus subtorta* were collected from Dee Why lagoon, near Sydney, New South Wales, Australia, during May 1979. Dissections were undertaken in the laboratories of The Australian Museum, Sydney, and ciliary currents elucidated using carmine suspended in 50% sea water. Material was fixed in 5% formalin, sectioned at 6 μ and alternate sections stained in Ehrlich's haematoxylin and eosin or Masson's trichrome. Other sections of the mantle margin were stained in Conn's Safranin and Fast Green and Darrow's Safranin and Anilin blue for cellulose. Teased "zooxanthellae" from the ventral mantle margin were also examined using a Nomarski differential interference contrast (DIC) microscope. Regrettably I have been wholly unable to obtain further material suitably fixed for electron microscopy.

TAXONOMY

The species here under consideration was originally described as *Modiolarca subtorta* (Dunker 1857). Subsequently the genus *Fluviolanatus* was erected by Iredale (1924) to separate a single species — *F. subtorta* — from other mytilids.

Laserson (1956) later described a second species — *F. amarus* — from Dee Why lagoon, near Sydney. This author considered Dunker's *F. subtorta* to be a northern species originating from Port Essington, in the Northern Territories, and to be anteriorly narrow. *F. amarus*, on the other hand, is a southern species and has parallel dorsal and ventral margins.

Gabriel (1962), however, records *F. subtorta* from S.E. Australia occurring "on weed in coastal lagoons". Gabriel, moreover, considers the type to be *Modiola subtorta* Reeve 1858 (non Dunker). Soot-Ryen (1969) considered the correct name to be *F. subtorta* Dunker 1856 (1857). The occurrence of two very similar species in S.E. Australia, sharing a similar habitat, seems unlikely. *F. amarus* is probably thus but a junior synonym of *F. subtorta*, the two "species", in reality, no more than two extremes of the morphological range in shell form.

Dr. F.E. Wells of the Western Australian Museum has sent me material of *F. amarus* from Western Australia and I am convinced that the two species are conspecific.

BIOLOGY

Fluviolanatus subtorta occurs in estuaries and coastal lagoons and appears to extend all

along the eastern coastline of Australia from the south eastern tip to the north eastern Northern Territories (Laseron, 1956).

Specimens of *F. amarus* (here considered conspecific with *F. subtorta*) have also been received from Western Australia. At Ravenswood in the Murray River, 80 km south of Perth, the species occurs in dense populations on logs and is associated with *Xenostrobus securis* (F.E. Wells, personal communication).

At Dee Why lagoon near Sydney where the specimens here reported upon were collected the species was found byssally attached to the stems of the surrounding fringe of reeds and to the algal mat (possibly *Hypnea* sp.) and any other solid substrate on the shallow lagoon floor. Associated with *Fluviolanatus* was, also byssally attached, the mytilid *Xenostrobus securis*. The biology of the latter species has been described by Wilson (1967). In the mud occur the burrowing bivalves *Psammobia onuphria* and *Arthritica helmsii*. Crawling over the surface of the mud were the two snails *Salinator fragilis* and *Hydrobia buccinoides*. This molluscan assemblage clearly points to an estuarine environment. The lagoon is intermittently inundated by fresh water and on occasion by sea water. I can find no information on the hydrology or ecology of these coastal lagoons.

FUNCTIONAL MORPHOLOGY

The shell and ligament

The shell of *Fluviolanatus* (Fig. 1A) is inequivalve and inequilateral. Generally, though very variable in form, the shell is roundly rectangular with the right valve somewhat larger than the left, the latter enclosed marginally by the former. Everywhere except for a slight gape posteriorly the valves meet when apposed; there is thus no byssal notch. Dorsally (Fig. 1B), the valve margin is straight but ventrally it is sinusoidally curved (Fig. 1C and E). The shell is markedly inequilateral resulting in the assumption of the heteromyarian form, the anterior face of the shell being reduced and the posterior enlarged. The large and flat umbones are sub-terminal and pointed forwards (Fig. 1D). The dorsal margin of the shell is slightly arched, the ventral margin variably either flat, inflated or depressed. The shell is very thin and a translucent brown. The underlying tissues are also heavily pigmented brown. Up to three lighter brown rays diverge from the umbones to the posterior margin of the shell and a further light ray extends ventrally from the umbones to the point where the byssus emerges from between the valves. Both the colour patterning and the shape of the shell is, however, extremely variable and almost certainly *F. amarus* is but a form of *F. subtorta* as discussed earlier.

Internally, the shell is brown with distinct pallial and muscle scar impressions. The ligament (Fig. 1F, L) is internal, opisthodontic, thin and located on weak nymphs. There are no hinge teeth and the umbones are slightly separated. Serial sections of the primary ligament (Fig. 2) show that it comprises a thick posterior outer ligament layer (POL) overlying a ventrally curved inner ligament layer (ILL). The anterior outer ligament layer, if at all present, is very much reduced. Dorsally, the primary ligament and the postero-dorsal regions of the shell are united by a thin layer of fused periostracum. Behind the umbones the primary ligament is split (Fig. 2D-H) this resulting from a weak tangential component of growth (Owen, 1958).

Seen from the anterior and posterior aspects (Fig. 1D and F), the enclosing nature of the right valve is more apparent as is the curvature of the ventral margin. It can also be seen that the greatest width of the shell is somewhat dorsal to the mid dorso-ventral axis of the shell and the form is thus typical of many nestling heteromyarian bivalves e.g. *Modiolus*, *Philobrya*, *Gaimardia* and *Trapezium* (Morton, 1977; 1978a; 1979, a;b).

Internally (Fig. 1F), the pallial line (PL) is thick and deeply recessed between the valves. There is a shallow pallial sinus (PS). The anterior adductor muscle (AA), located on the anterior face of shell, is round in outline and only slightly smaller than the posterior adductor (PA) which is located on the postero-dorsal edge of the shell. Internal to each is anterior and posterior byssal retractor muscles (ABR:PBR), the former smaller than the latter.

Dr. J.D. Taylor of the British Museum (Natural History) has kindly examined the shell structure of specimens of *F. subtorta* and shown it to comprise an outer crossed-lamellar layer and an inner complex crossed-lamellar layer.

The mantle

Each mantle lobe comprises three folds. Mantle fusion between the exhalant and inhalant siphons and between the inhalant siphon and the pedal gape is of the inner folds only and thus of type A (Yonge, 1957; Stanley, 1968). Dorsally, mantle fusion progressively involves further folds until with the fusion of the inner surfaces of the outer mantle folds, there is formed a continuous secretory epithelium and thus a layer of fused periostracum.

Seen in tranverse section, the mantle margins comprise fused inner folds, posterior to the pedal gape (Fig. 3 FIMF), that are weakly cross invaded by pallial retractor muscles (PM). The middle fold (MMF) is extremely small whereas the outer fold is very large (OMF). The inner surface of the outer fold secretes the periostracum (P) which comprises two layers (Fig. 4). An inner layer (IP) stains blue in Masson's trichrome, whereas an outer layer (OP) stains red. The latter is somewhat fringed and to it is attached a luxuriant growth of algae and diatoms in particular. The outer fold also possesses an enormous haemocoel that contains large numbers of what appear to be algal cells (Figs. 3, 4, 5, 6). The cells (Z), seen in greater detail in Figure 5, are round or polygonal, possess a thin, smooth, outer coat lacking pores or reticulations as revealed by examination of smears using Nomarski optics. The cell walls and assimilation product stain positively for cellulose in Conn's and Darrow's stain, the cytoplasm colourless. The cells, without flagellae and thus vegetative (VC), are 6-8 μ in diameter with an irregular, brown, assimilation product (AP); some 2 μ in diameter, linked to the outer cell wall. The nucleus (N) is indistinct and the cytoplasm contains a few cell inclusions such as oil droplets (OID) and vacuoles (VA). Younger, smaller cells (YVC) are more darkly staining but still with a distinct assimilation product (AP) and chloroplasts (CH). These structures are not molluscan amoebocytes or granulocytes (Cheney, 1971) or eggs. The cells are wholly unlike *Chlorella* recorded from the mantle of *Anodonta cygnea* (Goetsch and Scheuring, 1926) but remarkably similar to vegetative "zooxanthellae" (*Symbiodinium microadriaticum*) recorded from a wide range of coelenterates but especially hermatypic, scleractinian corals and giant clams of the genera *Tridacna* and *Hippopus* and illustrated by McLaughlin and Zahl (1966; Figs. 1, 4, 7 and 8). The final decision as to the status of these cells in the mantle margin of *Fluviolanatus* must be left to other local scientists, as I have been unable since this research was undertaken in 1979 to obtain further material fixed for electron microscopy. If they do ultimately prove to be "zooxanthellae" as I believe, the physiological consequences for them and *Fluviolanatus* must also be investigated. Some discussion of this question will follow.

The inner mantle fold possesses glands discharging onto the inner surface of the mantle. Posteriorly (Figs. 3 and 7b; EXC (2)) these are epithelial, anteriorly (Figs. 6 and 7a; EXC (1)) they are sub-epithelial. Possibly they secrete mucus to assist in pseudofaeces consolidation and discharge.

The siphons

The siphons (Fig. 8) are formed by fusion of the inner mantle folds only and are densely pigmented brown. Although the pallial sinus itself is shallow, the pallial line is deeply recessed between the shell valves and the siphons can thus be deeply withdrawn. The siphons are extremely sensitive, rarely fully expanding. The exhalant siphon (Fig. 9A, ES) is small and in the form of a cone. The inhalant siphon (IS) is much larger and at its apex bears a crown of papillae arranged in two cycles. An inner ring of approximately sixteen large tentacles is surrounded and interspersed by an outer cycle of smaller papillae. Surrounding the base of each siphon laterally are found a series of much larger tentacles that also extend dorsally. As the mantle folds progressively fuse these become smaller. Siphons and tentacles are pigmented brown, the larger tentacles possessing a white ring at their apex.

The ctenidia and labial palps

The ctenidia of *Fluviolanatus* (Fig. 9A) are exceptionally large, eulamellibranch, homorhabdic and non-plicate. The outer demibranch (OD) is much shorter than the

inner (ID). The ascending lamellae of both the outer and the inner demibranchs attach to the visceral mass by tissue union. The ciliary currents of the ctenidia are of type C (1) (Atkins, 1937) and thus typical of many lamellibranch bivalves. Acceptance tracts are thus located in the ctenidial axis and in the ventral marginal food groove of the inner demibranch only (Fig. 9B).

In section (Fig. 10) each filament is of simple structure and comprises three apical cells possessing a fringe of frontal cilia (FC) 5μ in length. These are flanked on either side by a cell possessing longer (12μ) eulatero-frontal cilia (ELFC) and with, characteristically, a very large (6μ) nucleus. External to this is a single non-ciliated cell. The sides of each filament comprise large cells that possess stiff lateral cilia (LC) which are approximately 18μ in length. Internal to the lateral cells are non-ciliated, flattened cells of the filament base enclosing the filament blood vessel (BV). Each filament is supported by thick "chitinous" rods (CR) and cross-connected by transverse fibres (TF).

The ctenidial-labial palp junction is of category III (Stasek, 1963) and the anterior end of the inner demibranch only projects between the ridged inner surfaces of the palps. The palps (Fig. 9A, LP) are exceedingly small and in the largest individuals never comprised more than 7 or 8 parallel ridges and grooves.

The mouth is located close to the postero-dorsal edge of the anterior adductor muscle and overlies the anterior byssal retractor muscles. The lips of the mouth are small and fleshy.

The ciliary currents of the mantle and visceral mass

The ciliary currents of the mantle (Fig. 11) are directed forwards and downwards on the dorsal regions. Ventrally, the ciliary currents are directed downwards and backwards passing unwanted material into a major rejectory tract on each mantle lobe and which extends posteriorly along the fused inner mantle folds towards the inhalant siphon (IS). Pseudofaeces travelling along these ciliated rejection tracts are presumably bound up in the mucus produced by the pallial glands (Fig. 7, EXC (1); EXC (2)) of the inner mantle folds and are eventually discharged from the inhalant siphon.

On the visceral mass (Fig. 12), the ciliary currents arise from a postero-dorsal focus and send material either antero- or postero- ventrally. In the former case particles are swept forwards and eventually downwards towards a major rejection tract located on the ventral region of each side of the visceral mass. In the latter case particles are swept backwards and downwards and fall from the visceral mass from its posterior border. On the general surface of the visceral mass therefore particle movement is ventral supplying a rejection tract that removes material from the visceral mass and on to the floor of the fused inner mantle folds.

The musculature, foot and byssus

The anterior adductor muscle (Fig. 12, AA) is located on the anterior face of the shell and is slightly smaller than the posterior adductor (PA) which is located close to the postero-dorsal margin. Internal to each adductor muscle is a single byssal retractor muscle (ABR:PBR), the anterior being considerably smaller than the posterior.

The foot (F) is relatively large and divided into a small "heel" and a greatly elongate "toe" that protrudes through the small pedal gape (PG) during locomotion. There is an extensive byssus gland dividing "heel" and "toe" and this secretes a small byssus (BY) that separates into short threads. The byssal groove (Fig. 13A, BGR) is located ventrally and the sole of the foot possesses an extensive sub-epithelial gland (PEG) that presumably secretes mucus. Seen in longitudinal section the byssus groove comprises a deep invagination, surrounded by the sub-epithelial cells of the byssus gland (BG) that stain positively in light green. Around the periphery of the foot the sub-epithelial mucous gland stains only very lightly in light green. In transverse section the byssus groove is thrown into a number of radially arranged cords which increase the surface area of the secretory tissue but which also serve to anchor the byssus into the visceral mass. The byssal retractors (ABR; PBR) diverge in the foot. The musculature (PEM) of the foot is not well defined and comprises an

outer layer of circular muscle internal to which are the longitudinal muscles of the byssal retractors, and radial muscles. The haemocoel of the foot possesses a few "zooxanthellae". Located within the foot, below the posterior byssal retractors are the pedal ganglia connected to the cerebropleural ganglia by the cerebropleural-pedal connectives (CPC). Antero-lateral to the ganglia are a pair of statocysts (Fig. 13B, SC). Each statocyst is some 30 μ in diameter and contains a solid, circular statolith (ST) 6-8 μ in diameter.

The alimentary canal

The stomach (Fig. 14, S) is located under the ligament and is surrounded by the dark mass of the digestive diverticula (DD). The oesophagus (Fig. 14, O; Fig. 16A) is a flattened tube some 150 μ in diameter and comprises a columnar epithelium, on average 20 μ in height that is thrown into a number of pleats. The cells are fringed by cilia 6 μ long.

The oesophagus opens into the stomach on its antero-ventral border. The stomach (Fig. 15) is small and globular and of Type V (typical of the Eulamellibranchia) (Purchon, 1958a; 1960). The descriptive stomach terminology of Purchon is used here. From its postero-ventral border arises a conjoined style sac and mid gut (CSM) that very quickly separate. From the style sac arises the major typhlosole (TY) accompanied along its right border by the intestinal groove (IG). The major typhlosole sweeps across the floor of the stomach to penetrate the right caecum (RC). It emerges from this caecum, traverses the anterior floor of the stomach from right to left and penetrates the left caecum (LC). The typhlosole emerges from this aperture to terminate on the floor of the stomach. Into the left and right caeca open the ducts to the digestive diverticula. Above the left caecum is located the left pouch (LEP) which engages a cusp of the gastric shield (GS) in its orifice. Curving around the posterior edges of the left pouch and caecum is a sorting area (SA6). The gastric shield is large and covers the left and postero-dorsal regions of the stomach. Against it rotates the crystalline style (CS) that emerges from the style sac (SS). From the mid gut (MG) arises the minor typhlosole (MT) that extends along the right wall of the stomach to terminate above the right caecum. Extending up the right side of the stomach and arching over to pass material into the dorsal hood (DH) (whose orifice is located on the left, antero-dorsal face of the stomach) is a ciliary tract. This is supplied posteriorly by sorting area SA3 and fed anteriorly by sorting area SA7 which arises on the floor of the stomach, under the aperture of the oesophagus, to pass up the right side, over the roof and into the dorsal hood. From the dorsal hood arises an elevated ridge (EL) that removes material from this cavity to take it to the posterior region of the stomach close to the aperture of the mid gut.

Thus, material entering the stomach is caught up by the crystalline style and presumably subjected to the extra-cellular digestive processes of this organ (Morton, 1973). Large particles fall onto the floor of the stomach where they are channelled into the intestinal groove (IG) by strong cilia on the surface of the major typhlosole. Small particles, in suspension, can enter the left and right caeca and the left pouch to be taken up by the digestive diverticula and subjected to the second process of intra-cellular digestion in this organ. Particles of intermediate size are collected by the sorting areas of the stomach (all of type A (Reid; 1965) and either accepted (as by, for example, sorting area SA6) or are recirculated, some being brought back into contact with the dissolving head of the style and if still of too large a size, rejected.

The style sac passes into the visceral mass and in transverse section comprises a number of epithelial zones earlier recognised by Kato and Kubomura (1954) and Morton (1969). The style sac (Fig. 16D) is 140 μ in diameter and largely comprises a uniform columnar epithelium of cells 10 μ tall with cilia 10 μ long (the A cell layer). The major typhlosole, the B cell layer, comprises cells 22 μ tall with a centrally located, elongate nucleus and cilia 4 μ long. A longitudinal "gutter" (G) in the style sac is flanked on one side by the C cell layer (which corresponds to the intestinal groove) and comprises cells 6 μ tall with cilia 8 μ long. The opposite side of the "gutter" comprises the D cell layer (D) of cells 6 μ tall with cilia 8-10 μ long. In *Dreissena polymorpha* (Morton, 1969) a style sac of similar structure is found and the D cells secrete the style matrix.

The separated mid gut (Fig. 16B) comprises a narrow tube $100\ \mu$ in diameter that possesses the minor typhlosole forming a large epithelial inpushing in the lumen. The epithelial cells are on average $20\ \mu$ tall, with a basal nucleus and cilia $8\ \mu$ long. The mid gut loses the typhlosole and forms a simple tube — the hind gut (Fig. 16C) — uniformly composed of an epithelium $14\ \mu$ tall fringed by cilia $10\ \mu$ long. The gut penetrates the heart as the rectum (Fig. 16E). In so doing the diameter is considerably reduced to $60\ \mu$ and the epithelium is thrown into a number of longitudinal pleats. The epithelial cells are $10\ \mu$ in height, with a basal nucleus and very long cilia ($10\text{--}12\ \mu$). The rectum passes over the kidney (Fig. 14, K), between the posterior byssal retractors (PBR) and over the posterior adductor (PA) to terminate on the posterior face of this muscle in an anus (AN).

The digestive diverticula of *Fluviolanatus* (Fig. 16F) are of the typical elumellibranch structure as described by Owen (1955) and by Morton (1970a; 1973; 1980b) in a number of studies of a variety of bivalves. The digestive tubules comprise two cell types: digestive cells (DC) form the sides of the tubule, are some $20\ \mu$ in height and in the collected specimens, possessed large amounts of food material enclosed within intra-cellular vacuoles and staining positively in light green. Ranks of digestive cells are separated by clusters of conical crypt cells (CC) which Morton (1970a) has shown to possess a regenerative function and which stain positively in acid fuchsin. From these cells are also arise long ($25\ \mu$) cilia (CI).

The pericardium

The pericardium (Fig. 15 PER) is located posterior to the ligament and contains a heart which comprises a single ventricle (V) and single anterior and posterior aortas. Laterally are a pair of thin walled auricles (AU). From the posterior face of the pericardium arise the paired kidneys. Each proximal limb (PK), arising from a renopericardial aperture (RPA) is a narrow tube some $30\ \mu$ in diameter and comprising a cuboidal epithelium $5\ \mu$ tall densely lined by cilia $12\ \mu$ long (Fig. 18C). This region of the proximal limb is unusually long and eventually opens into a non-ciliated region (Fig. 17, PK (NC)) that comprises a long, deeply folded tube composed of unciliated, columnar cells $15\ \mu$ tall with apical cilia and a fringe of microvilli (Fig. 18B, MI). The proximal limbs are located under the paired distal limbs (Figs. 15 and 17, DK) and posteriorly the former divide and communicate with the latter which extend over and around (but do not enclose) the proximal limbs. The distal limbs (Fig. 18A) comprise a columnar epithelium, with highly vacuolated cells $20\ \mu$ tall possessing a basal nucleus $4\ \mu$ in diameter but also possessing, distally, an excretory concretion (EC) $5\ \mu$ in diameter on average. Anteriorly, left and right distal limbs fuse and eventually open into the supra branchial chamber on each side via a small excretory duct and renal aperture (Fig. 15, RA). The excretory aperture is located close to a small gonadial aperture (GA) arising from the gonads. *Fluviolanatus subtorta* is dioecious the gonads extending around the visceral mass and dorsally into the mantle.

DISCUSSION

Interest in *Fluviolanatus subtorta* is from two major points of view. The first concerns its affinities with the remainder of the Bivalvia. Hitherto the genus has been located in the Mytilacea (Iredale, 1924; Laserson, 1956; Soot-Ryen, 1969) but the possession of a eulamellibranch ctenidium clearly precludes association with this superfamily, indeed with the Pterioidea altogether. Of the remaining orders of bivalves, a trend towards a heteromyarian form occurs in representatives of the Myoida, Pholadomyoida and the Heterodonta. In the Myoida there is a general tendency towards deep burrowing and the mantle fusions typically involve more than the inner folds and the siphons are long and fused. Similarly, approximately heteromyarian bivalves occur in the Lyonsiidae of the Pholadomyoida (*Anomalodesmata*) (Yonge, 1952; Narchi, 1968; Morgan and Allen, 1976). Of especial interest here is the fresh water, heteromyarian lyonsiid (*Guianadesma sinuosum* (Morrison, 1943)). In these bivalves, however, the ctenidia lack the ascending lamella of the outer demibranch and the ctenidial ciliation is thus of type E (Atkins, 1937). The mantle margins are again extensively fused, often with a fourth pallial aperture. *Fluviolanatus* lacks all the anomalodesmatan features recently reviewed by Morton (1981a).

It thus seems likely that *Fluviolanatus* should more correctly be assigned to the Heterodonta and amongst this assemblage, only a few phylogenies possess heteromyarian representatives. These include the Dreissenidae Gray in Turton 1840, the Gaimardiidae Hedley 1916 (regarded by Ponder (1971) as a sub-family — Gaimardiinae — of the Cyamiacea), the Trapeziidae Lamy 1920 and the Carditidae Fleming 1828. Important features of these four families are compared with *Fluviolanatus* in Table 1. Of the four families, the Dreissenidae can, on shell characters alone, be omitted. Members of this family (Morton, 1969; 1981b) characteristically possess a shell shelf (or septum or myophore plate) to which is attached the anterior adductor muscle and, to a lobe of this in *Mytilopsis*, the anterior byssal retractor muscle. Similarly, the ligament of *Dreissena* has been shown to be unique with a tongue of tissue extending above the primary ligament and secreting two separate layers of periostracum (Yonge and Campbell, 1968).

Separation of representatives of the other three families is usually possible on hinge teeth structure, but the absence of hinge teeth in *Fluviolanatus* precludes this criterion. The Gaimardiidae can, however, also be excluded because of their homogeneous shell structure (Taylor, Kennedy and Hall, 1973). For other reasons also the Gaimardiidae can be separated from *Fluviolanatus*. Gaimardiid bivalves are generally small and often related to the lucinid-leptonid line of evolution (Newell, 1965). In *Neogaimardia* there is an internal ligament whereas in *Gaimardia* and *Kidderia* it is either sub-internal or external. Similarly, although *Neogaimardia* possesses an inner demibranch only and thus has a gill ciliation of type D, species of *Perrierina*, *Kidderia*, *Anisodonta* and *Cyamium* possess both demibranchs and, in the case of *Anisodonta*, a gill ciliation of type C (1). *Anisodonta* is, however, non-byssate in the adult (Ponder, 1971). The siphons of all gaimardiids are exceedingly simple; there are no pallial glands and little is known of the stomach structure. Such information on the latter as is available comes from a study of *Turtonia minute* (Oldfield, 1955), a bivalve, like *Fluviolanatus*, of dubious affinity and located in the Cyamiacea close to the Gaimardiacea by Chavan (1969), but considered by Ockelmann (1964) to be a neotenous veneracean. Neoteny may be widespread in the group Cyamiacea/Gaimardiacea as a whole, however, since Morton (1979a) has suggested that many of the features of *Gaimardia* indicate neoteny leading to a simplicity of form and thus a greater degree of similarity.

Generally speaking, the Carditidae can be excluded for a number of fundamental reasons. The mantle margin of all carditiids is exceedingly simple with no fusion ventrally and with the siphons represented by simple orifices. Both demibranchs are present and the gill ciliation is of type D (Atkins, 1937) with a ctenidial-labial palp junction of category III (Stasek, 1963). Most important is that the stomach of the Carditidae is of type IV which it shares with the Gaimardiidae, i.e. *Turtonia* (Purchon, 1958a). Purchon (1958b) has shown most convincingly that different bivalve phylogenies possess stomachs of distinctive structure. The other bivalve families, and *Fluviolanatus*, here discussed have a distinctly different structure of Type V forcibly arguing for a separate general line of evolution. Yonge (1969) has further shown that the Carditidae is a relatively ancient group with a lucinid type heterodont hinge (having its origins in the Ordovician (McAlester, 1965)) and generally related to the Astartacea and thus to some of the most primitive Eulamellibranchia. *Fluviolanatus* with stomach type V is thus distinct from the Carditidae.

Fluviolanatus has finally been compared with representatives of the two major genera of the Trapeziidae. Until recently little was known of this group other than a taxonomic review by Solem (1954). *Trapezium* and *Coralliophaga* have, however, lately been investigated by Morton (1979b; 1980a). In these bivalves the shell is heteromyarian, with an internal ligament and, significantly, *Coralliophaga* is almost transparent. Ventral mantle fusion is extensive (inner folds only in *Trapezium*; inner and middle folds in *Coralliophaga*) and the siphons, notably the inhalant, possess complex siphonal tentacles. There are also distinct siphonal retractors. In *Coralliophaga*, the hinge teeth are much reduced as compared with *Trapezium*. The gill ciliation is of type C (1) in the Trapeziidae and *Fluviolanatus*, though in the former but not the latter, the ctenidium is plicate. Both have a stomach structure of Type V, the stomach of *Fluviolanatus* being very similar to that of *Trapezium sublaevigatum* (Morton, 1979b). One further point of similarity concerns

the paired statocysts. In *Coralliophaga* (Morton, 1980a) and *Fluviolanatus*, the statoliths are solid (hollow in *Gaimardia*) (Morton, 1979a) and although statocyst structure has never been studied on a comparative basis it is becoming clear that such structures do differ in different groups. The statocysts of *Pholadomya* are, for example, highly distinctive (Morton, 1980b). Thus although the absence of hinge teeth does preclude exact confirmation of the taxonomic position of *Fluviolanatus* many aspects of the anatomy ally it with the Trapeziidae. Also, as shown here, it is clearly not related to the other recognized families of heteromyarian, heterodonts. Generally, the Trapeziidae, except for the rare *Isorropodon* (Solem, 1954), are shallow water bivalves. *Coralliophaga* inhabits coral galleries, *Trapezium* is a nestler of sheltered rocky shores under an estuarine influence (Morton, 1979b; 1980a). *Fluviolanatus* has a comparable habit and it is easy to imagine a primitive ancestor in which the retention of the byssus, the assumption of the heteromyarian form (with a concomitant reorientation and overall reduction of the hinge teeth) has allowed the family to diversify into a number of niches.

Other important features of *Fluviolanatus* concern themselves with the adoption of the heteromyarian form. Thus the anterior adductor and anterior byssal retractor are reduced relative to their posterior equivalents and there is a corresponding reduction in the anterior face of the shell. The hinge plate becomes progressively reduced in sequences of heteromyarianisation as demonstrated for the Dreissenacea by Morton (1970b) and for the Mytilacea by Stanley (1972). The ligament also lengthens. In *Fluviolanatus*, the ligament is excessively small, and anteriorly, under the umbones, splits — this resulting from a weak expression of tangential growth as defined by Owen (1958) and also seen in the Carditidae (Yonge, 1969) but achieving full expression usually only in cemented bivalves e.g. the Chamidae (Yonge, 1967) and Cleidothaeridae (Morton, 1974).

Fluviolanatus possesses large ctenidia and small palps, not features of bivalves occupying sediment laden waters. Possibly the extensive sorting areas of the stomach compensate for the small palps. The alimentary canal is long and adapted for dealing with large amounts of small particles. The siphons are short, very sensitive and deeply recessed between the fragile shell valves. Clearly the latter feature is a protective device, but thin shell valves are typical of commensal (the Leptonacea as a whole) or deep burrowing, immobile bivalves (e.g. Laternulidae) (Morton, 1976) but not nestling species with the possible exception of *Coralliophaga* (Morton, 1980a). There is an anomaly here.

Possibly the most interesting feature of *Fluviolanatus* is the presence of what appear to be “zooxanthellae” in the greatly enlarged inner, but more especially, the outer mantle folds of the ventral mantle margin. These cells are located under the shell and periostracum and, moreover, in the ventral region of the mantle i.e. that region of the animal most closely applied to the substratum because of byssal attachment.

Typical of hermatypic scleractinian corals and giant clams, “zooxanthellae” (*Symbiodinium microadriaticum*) occur in those tissues most exposed to light. By their photosynthetic properties they possibly fulfil a number of functions, the most important of which in corals (Barnes, 1973) (and probably giant clams) is enhanced calcium deposition (Yonge, 1963). Clearly this is not so in *Fluviolanatus* with a reduced shell. The thin shell may, however, as in *Corculum* (Kawaguti, 1950; 1968), facilitate light penetration. The underlying mantle is deeply pigmented brown. Pigmentation of the mantle tissues may serve a dual function acting to reduce excessive light intensity and to alter light quality (Taylor, 1973). Spectral quality is an important factor in the determination of nutrient quality. Thus as spectral composition is shifted in favour of shorter wavelengths, there is an enhancement of protein synthesis relative to carbohydrates (Taylor, 1973). Reduced photosynthetic rates, due to reductions in available light, can have a profound effect on skeletal form (Barnes, 1973), while enhanced light intensities can suppress rates of calcification (Barnes and Taylor, 1973).

Possibly the thin shell of *Fluviolanatus* is a morphological compromise in which two opposing demands are attempted to be met: first, protection of the contained animal and, second, light penetration to enable to “zooxanthellae” to sustain photosynthesis. This is possible also the case in *Corculum* (Kawaguti, 1950; 1968).

The algae may constitute a reservoir of reduced organic carbon and essential nutrients (in the broadest sense of the word) that are available to the bivalve. Thus Fankboner (1971) has shown that in *Tridacna* the zooxanthellae are celled to be intra-cellularly digested by amoebocytes. Many are removed via the digestive diverticula into the stomach to be expelled from the anus though the enlarged kidneys also play a role in the removal of excess zooxanthellae (Morton, 1978b). The digestive diverticula of *Fluviolanatus* appear to be of the typical eulamellibranch type (Owen, 1955) and not specialised as in *Tridacna* (Morton, 1978b) for the removal of zooxanthellae. Possibly therefore *Fluviolanatus* is dependent upon the nutrients produced by the zooxanthellae rather than upon breakdown of the algal cells themselves. In *Corculum cardissa* (Kawaguti, 1950; 1968) the zooxanthellae are housed in the mantle and the ctenidia (the overlying shell is thin as in *Fluviolanatus*) but digested by the 'liver' (digestive diverticula).

One other asset that the "zooxanthellae" may confer concerns gaseous exchange. Thus under optimal conditions (and clearly as an *Anodonta* (Goetsch and Scheuring, 1926), *Corculum* (Kawaguti, 1950; 1968) and *Tridacna* (Morton, 1978b) where in every case the algae are bathed in the haemocoelomic blood, such conditions may be 'optimal') symbiotic algae tend to produce an excess of oxygen beyond that consumed during respiration.

Similarly, carbon dioxide produced by the bivalve may be utilized by the algae.

The reviews of algal-animal associations by McLaughlin and Zahl (1966), Taylor (1973; 1974) and Trench (1979) adequately demonstrate the benefits accrued by symbiotic algae. Typically, bathed in isotonic blood, exposed to light they also have readily available to them excreted nitrates and phosphates which provide a reliable supply of these factors typically limiting to algal growth. This will also be true of *Fluviolanatus* and its algae and it is significant that the bivalve's kidney is different from that of others. It is unusual in two respects. First the proximal limbs, arising from the renopericardial apertures lie *under* the distal limbs, the two limbs uniting posteriorly. In most bivalves the proximal limbs are located *within* (typically fused) distal limbs. In *Coralliophaga* (Morton, 1980a) the distal limbs surround but are not penetrated by the proximal limbs and it seems possible that *Fluviolanatus* is a morphological extension of this condition with the proximal limbs becoming so large as to separate from intimate contact with the distal limbs. Second, the proximal limbs of the kidney of *Fluviolanatus* comprise two distinct sections. Typically the proximal limb is a simple unciliated tube composed of cuboidal cells supplying the functional distal limb with pericardial fluids. (Only the renopericardial aperture and a short stretch of tube is ciliated). In *Fluviolanatus* the proximal limbs develop into capacious, deeply folded tubes composed of columnar cells bearing microvilli. The distal limb is of the typical bivalve type but the kidney cells possess excretory concretions also seen in *Tridacna* (Morton, 1978b), but also seen in other bivalves e.g. members of the Anomalodesmata (Morton, 1974; 1980b). If, and this seems likely, the "zooxanthellae" are utilizing the waste products of the bivalves metabolism, then the kidney may be functioning under redefined physiological parameters. Possibly also the algae release substances, not available to the host as food and which require, for excretion, a specialized renal apparatus.

This study cannot resolve the question of the precise relationship between *Fluviolanatus* and its symbionts. But it is hoped that this paper will stimulate local physiologists to investigate this unusual and enigmatic bivalve.

ACKNOWLEDGEMENTS

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ABBREVIATIONS USED IN THE FIGURES

A, A cell layer of the style sac; AA, Anterior adductor muscle (or scar); ABR, Anterior byssal retractor muscle (or scar); AN, Anus; AP, Assimilation product; AU, Auricle; B, B cell layer of the style sac (the major typhlosole); BG, Byssal gland; BGR, Byssal groove; BV, Blood vessel; BY, Byssus; C, C cell layer of the style sac; CA, Ctenidial axis; CC, Crypt cell; CH, Chloroplast; Cl, Cilia; CPC, Cerebropleural-pedal connective; CR, "Chitinous" rod; CS, Crystalline style; CSM, Conjoined style sac and mid gut; CVC, Cerebropleural-visceral connective; D, D cell layer of the style sac; DC, Digestive cell; DD, Digestive diverticula; DH, Dorsal hood; DK, Distal limb of the kidney; EC, Excretory concretion; EL, Forwardly projecting elevation on the right side of the stomach; ELFC, Eulatero-frontal cilia; EP, Epithelial cell; ES, Exhalant siphon; EXC (1), secretory cell type 1; EXC (2), secretory cell type 2; F, Foot; FC, Frontal cilia; FIMF: Fused inner mantle folds; FP, Fused periostracum; G, "Gutter" of the style sac; GA, Gonadial aperture; GS, Gastric shield; H, Heart; HG, Hind gut; ID, Inner demibranch; IG, Intestinal groove; ILL, Inner ligament layer; IMF, Inner mantle fold; IP, Inner layer of periostracum; IS, Inhalant siphon; K, Kidney; L, Ligament; LAC, Lateral cilia; LC, Left caecum; LEP, Left pouch; LP, Labial palp; M, Mantle; MG, Mid gut; MI, Microvilli; MMF, Middle mantle fold; MT, Minor typhlosole; N, Nucleus; O, Ovary; OD, Outer demibranch; OE, Oesophagus; OID, Oil droplets; OMF, Outer mantle fold; OP, Outer layer of periostracum, P, Periostracum; PA, Posterior adductor muscle (or scar); PALID, Line of attachment of the ascending lamella of the inner demibranch to the visceral mass; PBR, Posterior byssal retractor muscle (or scar); PE, Pedal gape; PEG, Pedal gland; PEM, Pedal musculature; PER, Pericardium, PG, Periostracal groove; PI, Pigment granules; PK, Proximal limb of the kidney; PK (C), Ciliated portion of the proximal limb of the kidney; PK (NC), Non-ciliated portion of the proximal limb of the kidney; PL, Pallial line; PM, Pallial musculature; POL, Posterior outer ligament layer; PS, Pallial sinus; R, Rectum; RA, Renal aperture; RC, Right caecum; RPA, Renopericardial aperture; RT, Rejactory tract; S, Stomach; SA3, Principal sorting area of the dorsal hood; SA6, The sorting area of the left pouch; SA7, The sorting area below the oesophageal orifice; SC, Statocyst; SH, Shell; SS, Style sac; ST, Statolith; TF, Transverse fibres; TY, Major typhlosole; U, Umbo; V, Ventricle; VA, Vacuole; VC, Vegetative cell; YVC, Young vegetative cell; Z, "Zooxanthellae".

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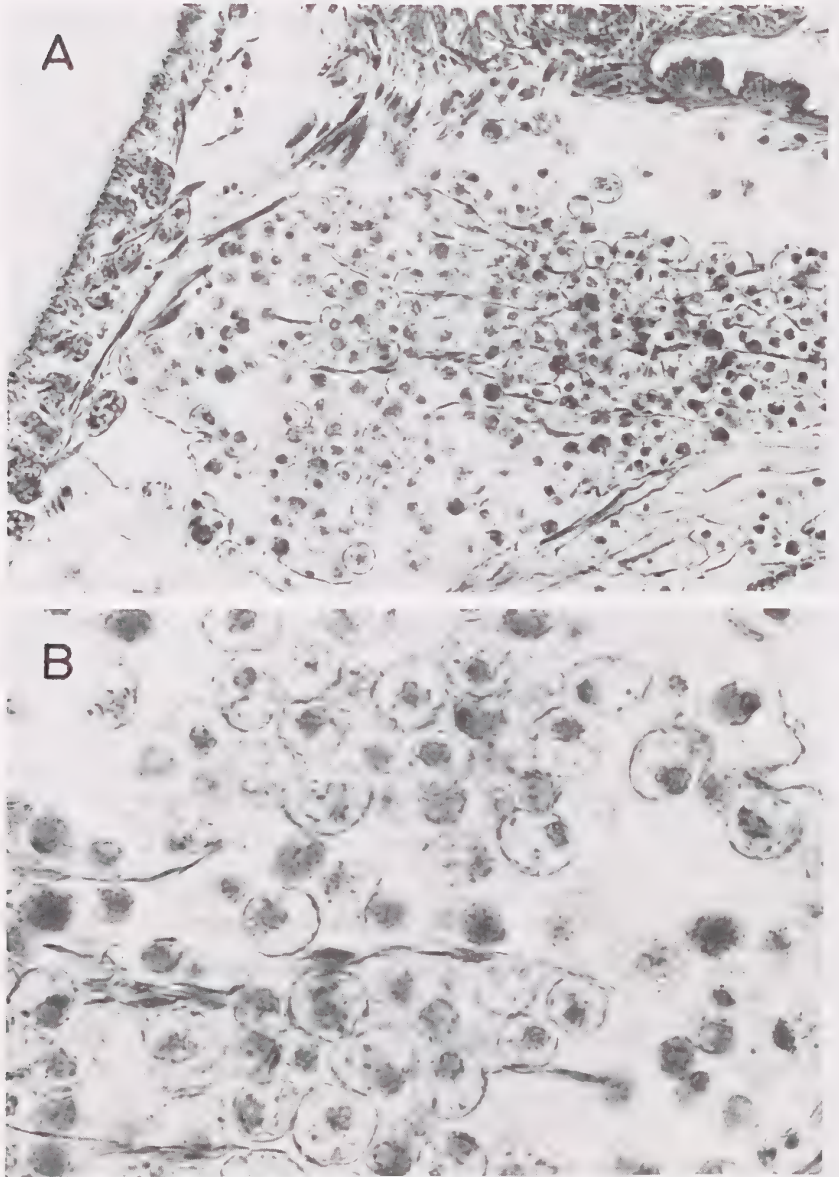


Plate 1. A, low and B, high power micrographs of the "zooxanthellae" in the outer mantle fold of the ventral mantle margin.

A comparison of important anatomical features of the Dreissenidae, Carditidae, Gaemardidae, Trapezidae, and *Fluviolanatus subortia*.
 TABLE 1

	1 Shell structure (Taylor, Kennedy and Hall, 1973)	2 Primary Ligament	3 Bysal notch	4 Shell thickness	5 Ventral mantle fusion (Yonge, 1957)	6 Well developed siphons	7 Pallial glands	8 Gill structure	9 Gill ciliation (Atkins, 1937)C (1)	10 Ctenial/labial palp junction (Stasek, 1963)	11 Style sac & mid gut	12 Stomach structure (Purchon, 1958a; 1960)	13 Statoliths
<i>Fluviolanatus</i>	(a) outer layer: crossed lamellar (b) inner layer: complex crossed lamellar	Internal (but with a complex structure (Yonge and Campbell, 1968))	Absent	thin (in <i>Coralliphaga</i>)	inner folds, but also middle in <i>Coralliphaga</i>	present	present	homorhabdic	C (1)	III	initially conjoined ultimately separate	V	solid
Trapezidae	crossed lamellar	Internal	Absent	thin (in <i>Coralliphaga</i>)	inner folds, but also middle in <i>Coralliphaga</i>	present	present	homorhabdic plicate	C (1a)	III	Conjoined	V	solid
Gaemardidae	homogenous structure	Internal	Present	Thick	inner folds	Absent	absent	homorhabdic non-plicate	G	III	Conjoined	IV in <i>Turtonia</i> (Oldfield, 1955)	hollow
Carditidae	crossed lamellar	External	Absent	Thick	None ventrally	Absent	Present	homorhabdic non-plicate	D	II	Conjoined	IV	—
Dreissenidae (Morton, 1969; 1981b)	crossed lamellar	Internal (but with a complex structure (Yonge and Campbell, 1968))	Present	Thick	inner folds	Present	Absent	homorhabdic non-plicate	D	III	Separate	V	—

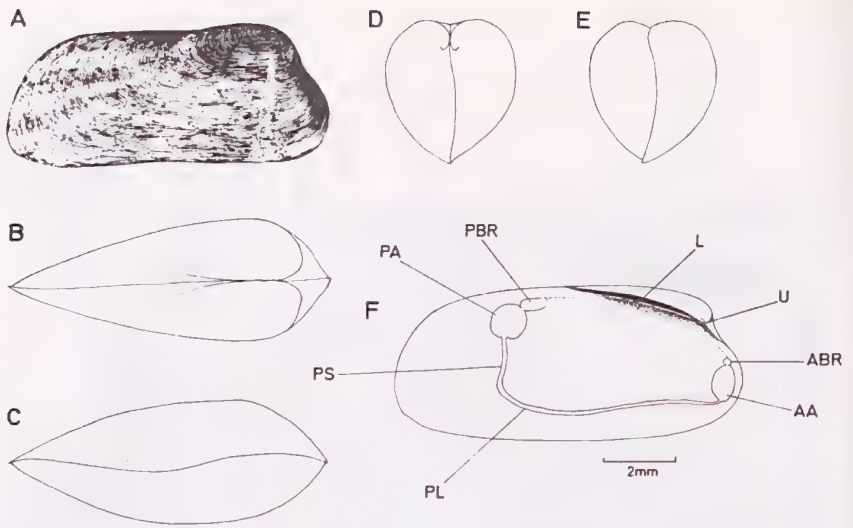


Figure 1. *Fluviolanatus subtorta*. The shell seen from A, the right side; and B, dorsal; C, ventral; D, posterior and E, anterior aspects; F, an internal view of the left shell valve. (For abbreviations see page 123).

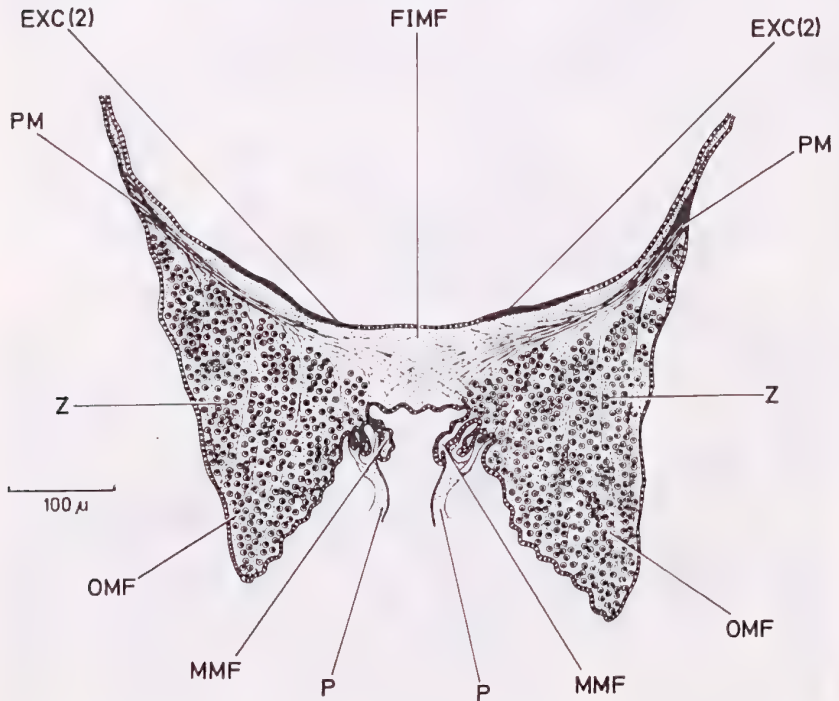


Figure 3. *Fluviolanatus subtorta*. A transverse section through the fused ventral mantle margin, posterior to the pedal gape. (For abbreviations see page 123).

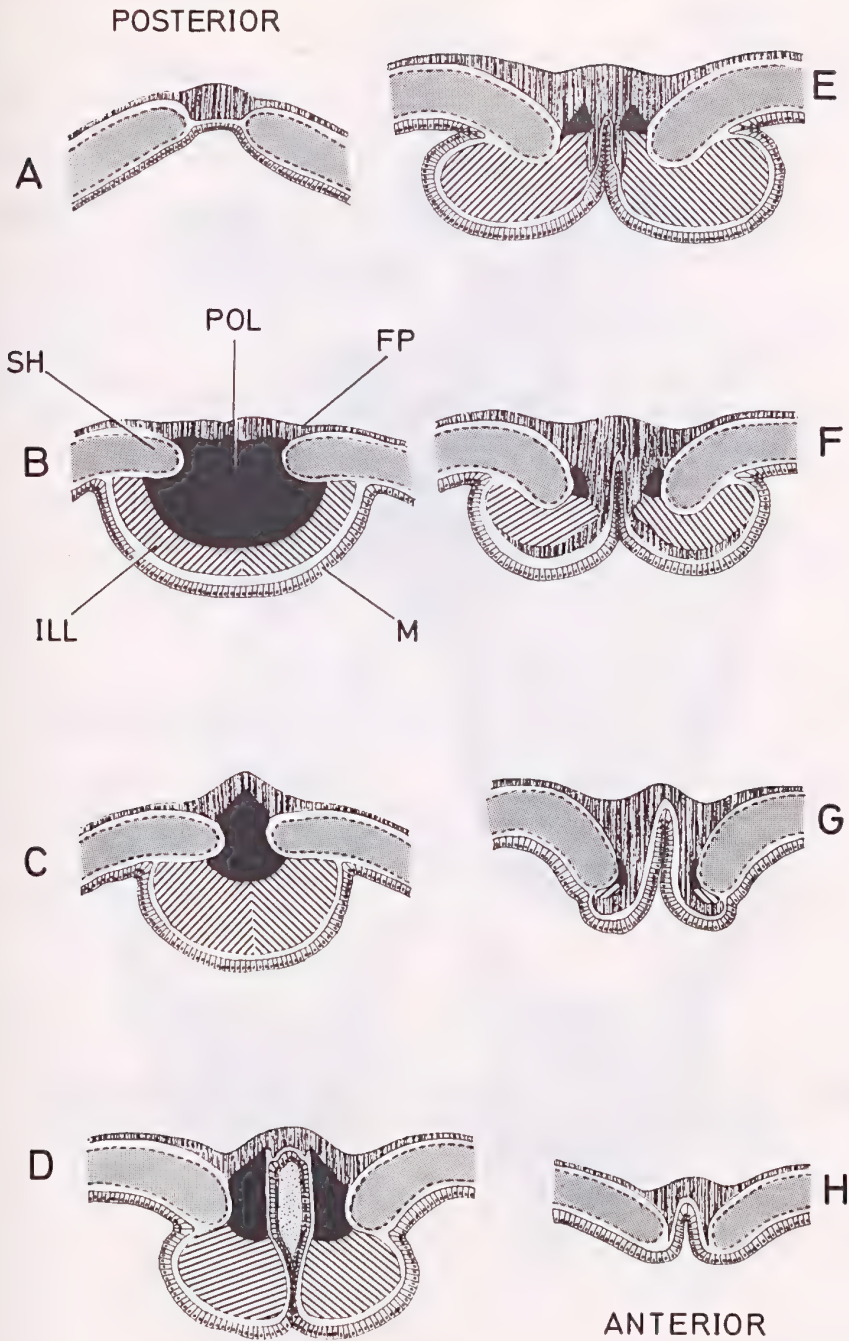


Figure 2. *Fluviolanatus subtorta*. Serial sections of the ligament from the posterior to the anterior. (For abbreviations see page 123).

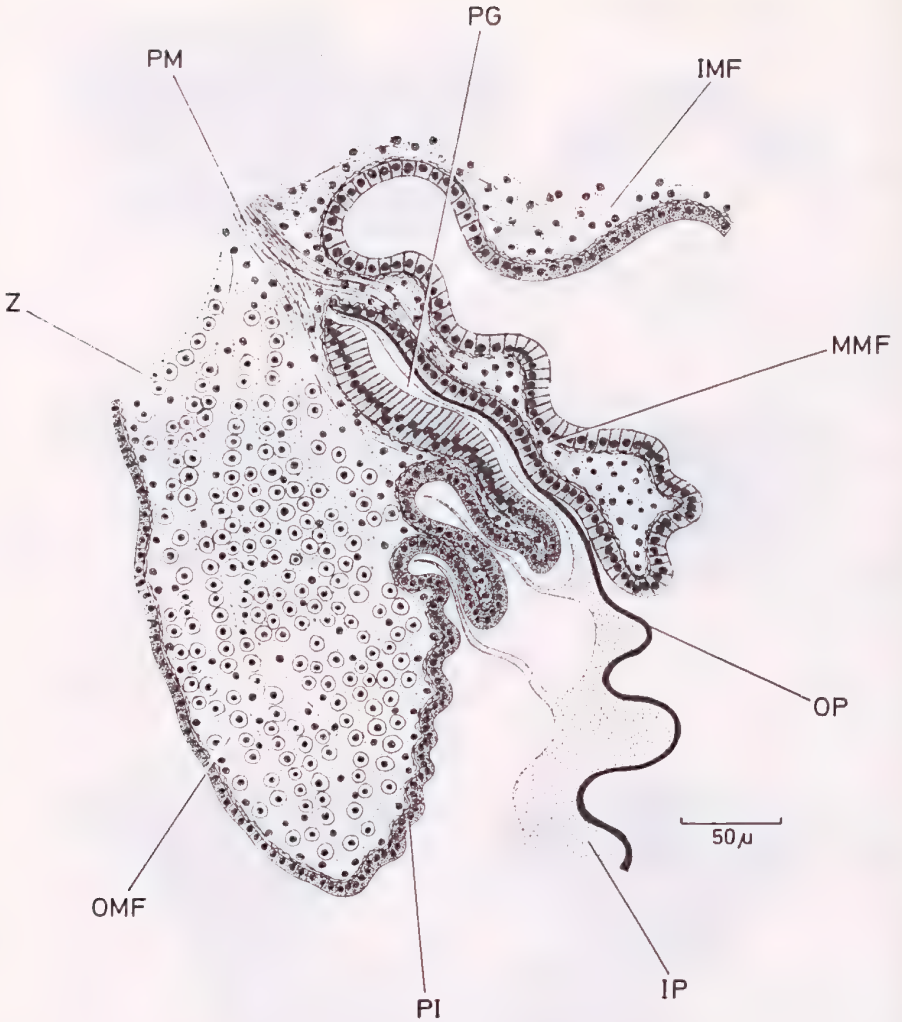


Figure 4. *Fluvianatus subtorta*. A detail of the ventral margin in the region of the pedal gape, showing the enlarged outer mantle fold full of "zoanthellae". (For abbreviations see page 123).

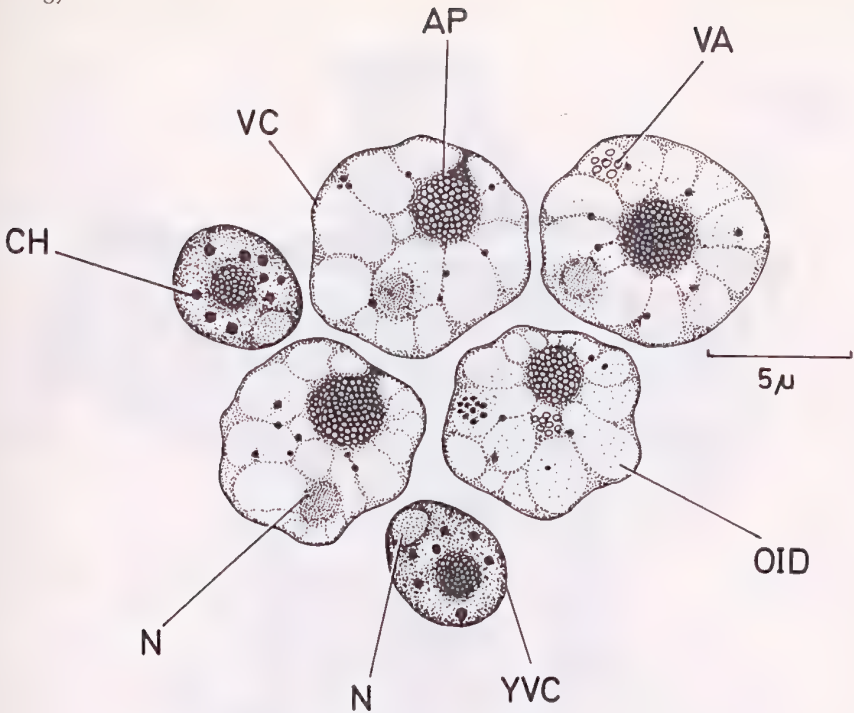


Figure 5. *Fluviolanatus subtorta*. Drawings of a number of "zooxanthellae" from the pallial haemocoel. (For abbreviations see page 123).

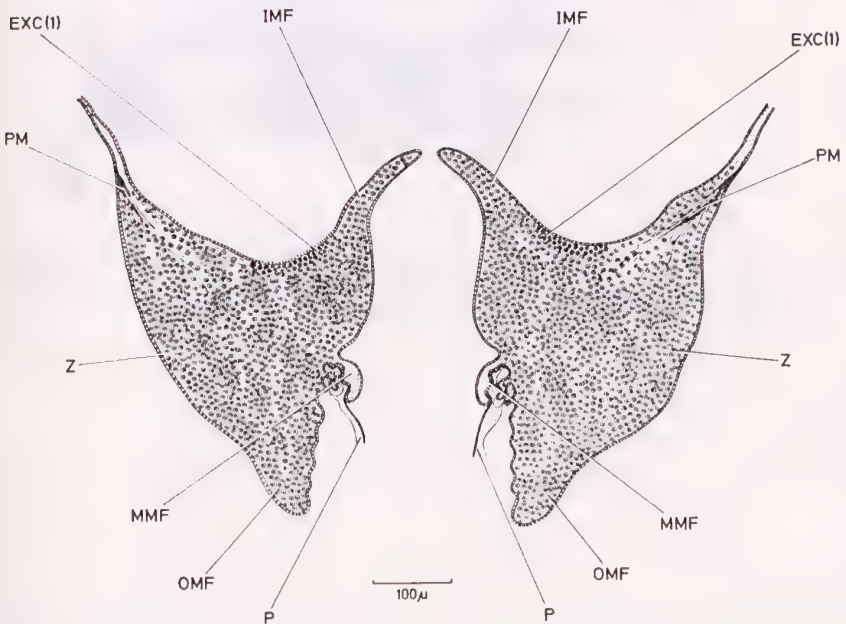


Figure 6. *Fluviolanatus subtorta*. A transverse section through the pedal gape. (For abbreviations see page 123).

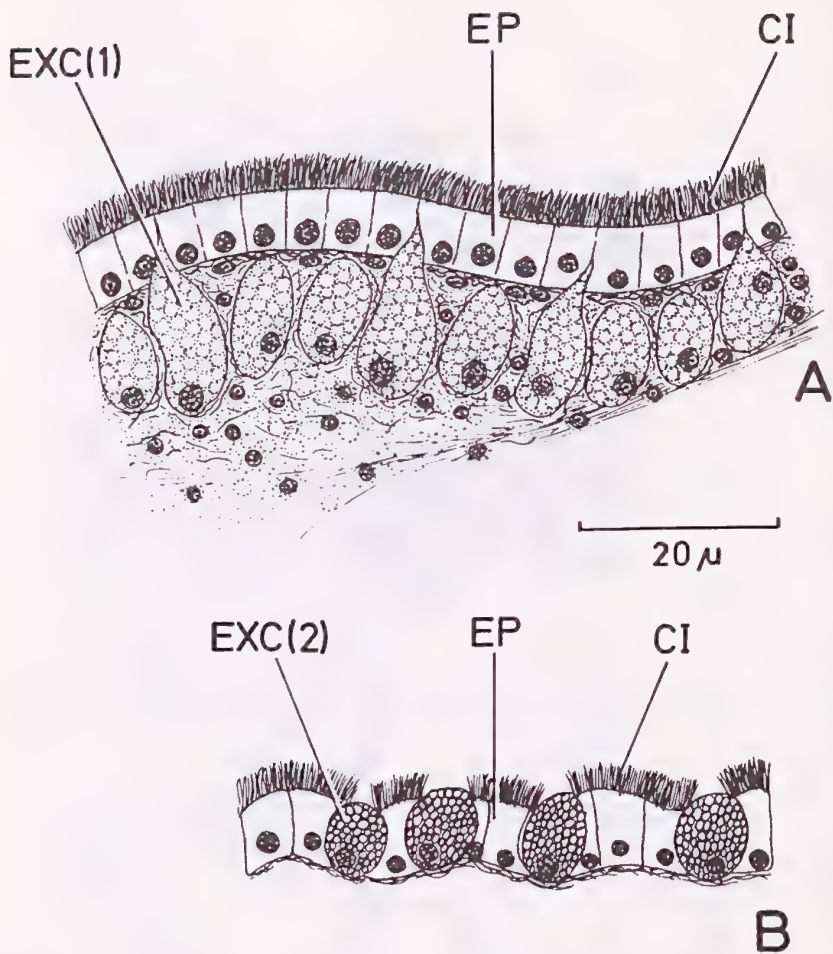


Figure 7. *Fluvianatus subtorta*. Sections through the inner epithelium of the inner mantle fold in the region of the pedal gape (A) and (B), posterior to the pedal gape. (For abbreviations see page 123).

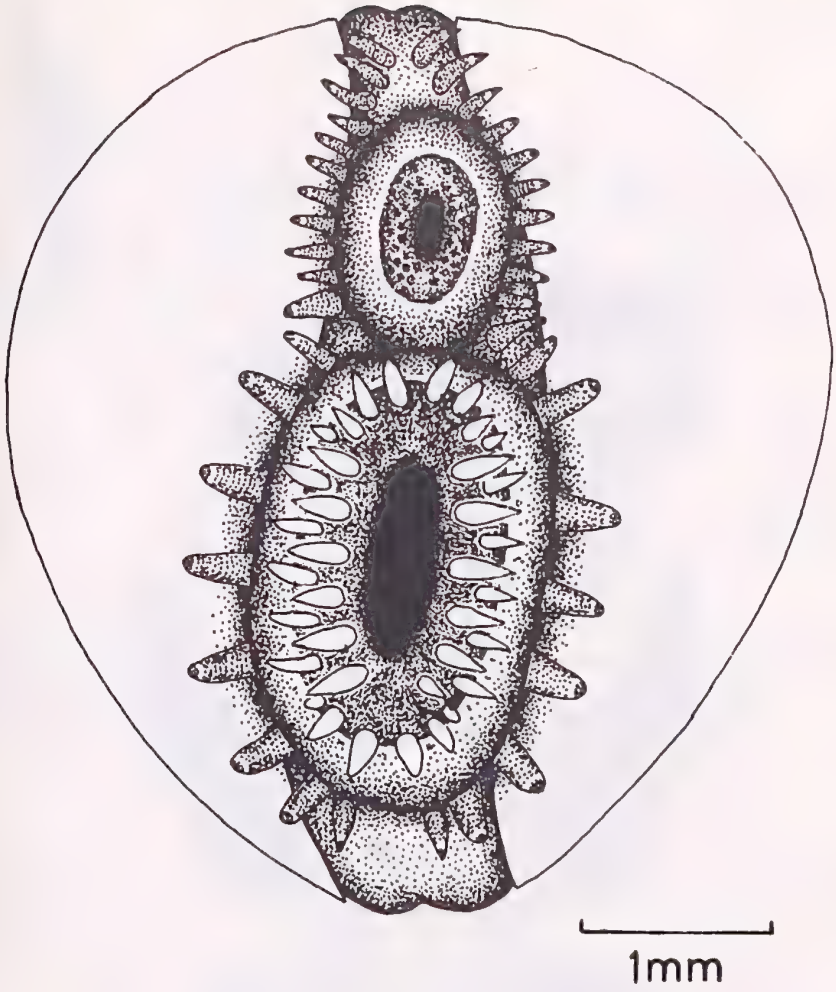


Figure 8. *Fluviolanatus subtorta*. The siphons as seen from the posterior aspect.

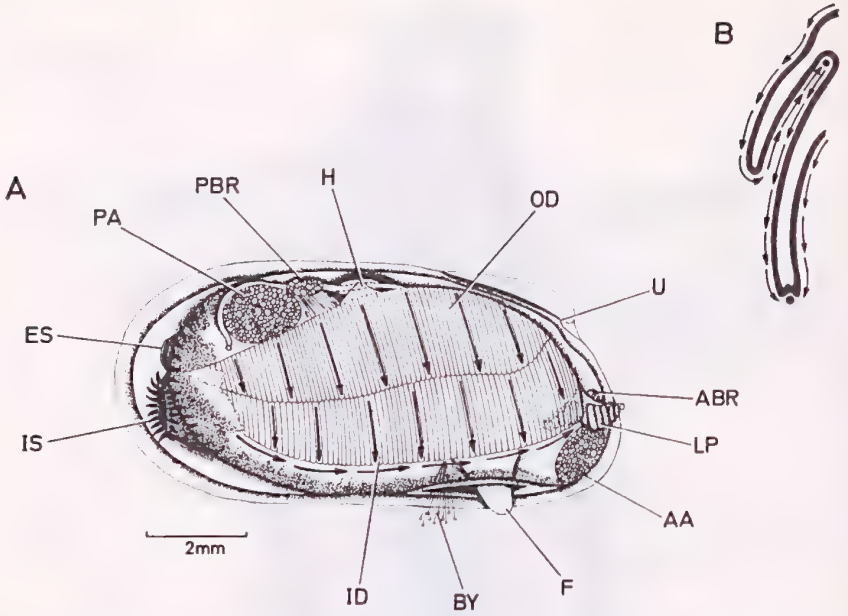


Figure 9. *Fluviolanatus subtorta*. A, The ctenidium as seen from the right side after removal of the right mantle lobe and shell valve. B, A transverse section through the ctenidium showing the ciliary currents. Black circles = acceptance tracts. (For abbreviations see page 123).

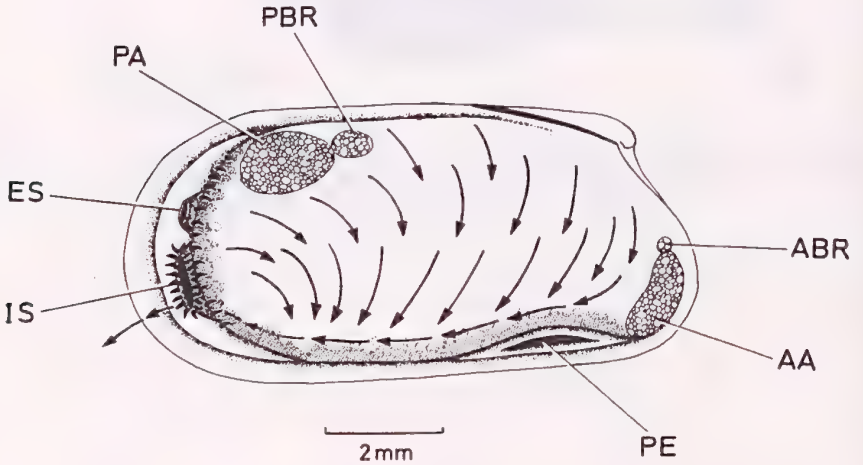


Figure 11. *Fluviolanatus subtorta*. The ciliary currents of the left mantle lobe. (For abbreviations see page 123).

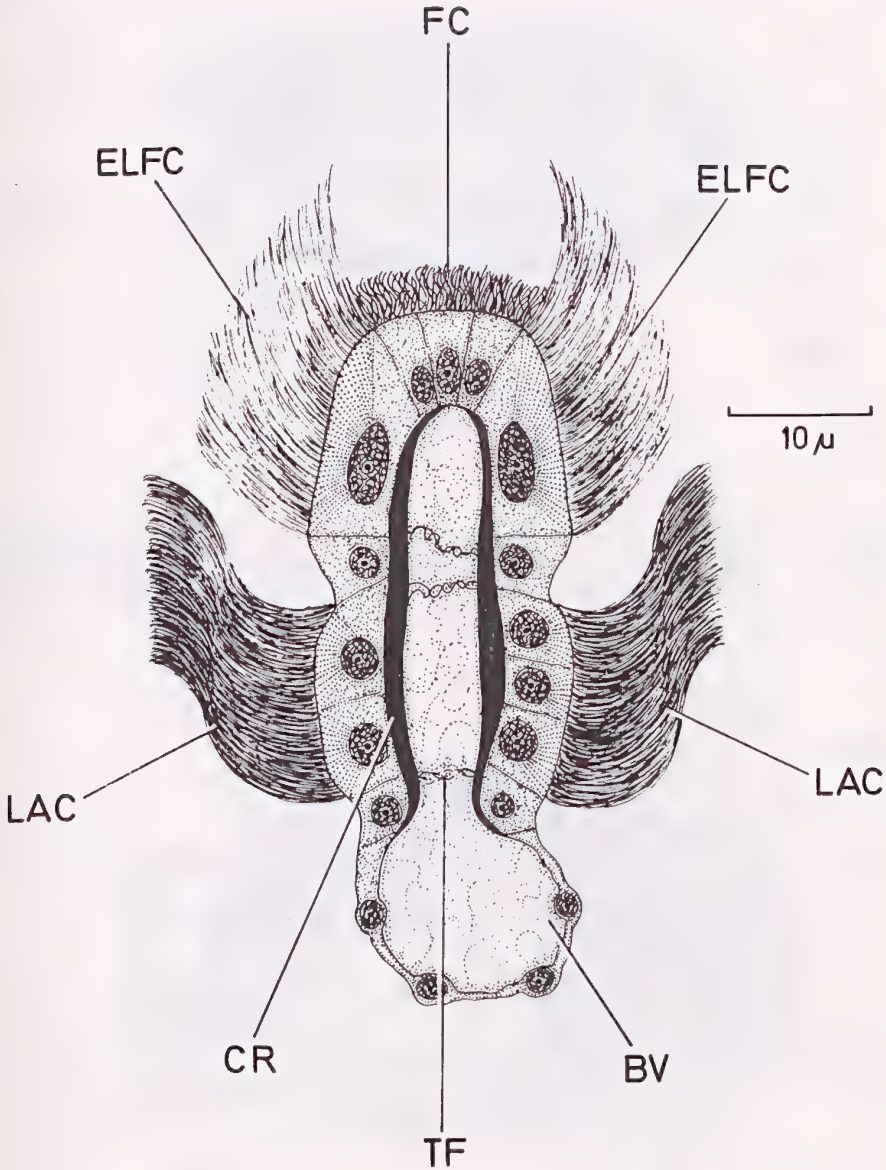


Figure 10. *Fluviolanatus subtorta*. A transverse section through a single ctenidial filament. (For abbreviations see page 123).

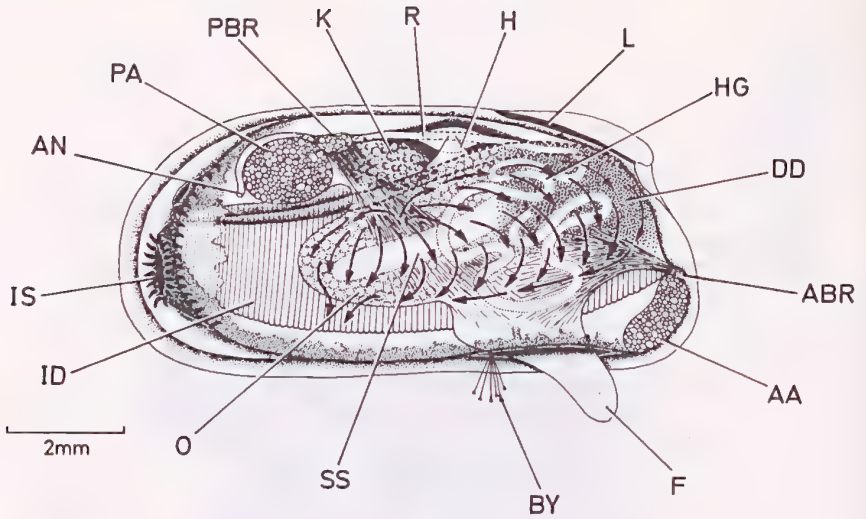


Figure 12. *Fluvioianatus subtorta*. The structure and ciliary currents of the visceral mass as seen from the right side after removal of the right ctenidium, mantle lobe and shell valve. (For abbreviations see page 123).

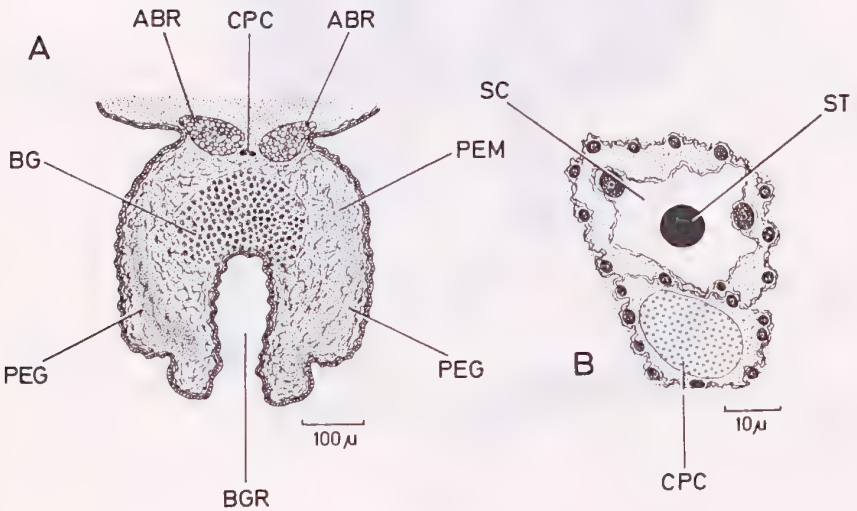


Figure 13. *Fluvioianatus subtorta*. A, A transverse section through the foot in the region of the byssal groove. B, A section through a single statocyst. (For abbreviations see page 123).

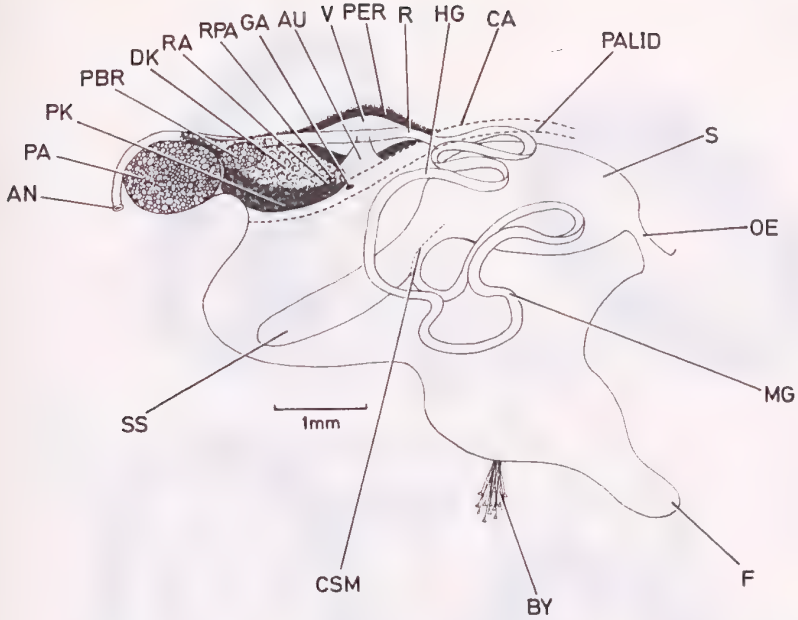


Figure 14. *Fluviolanatus subtorta*. The structure of the visceral mass with special reference to the organs of the pericardium. (For abbreviations see page 123).

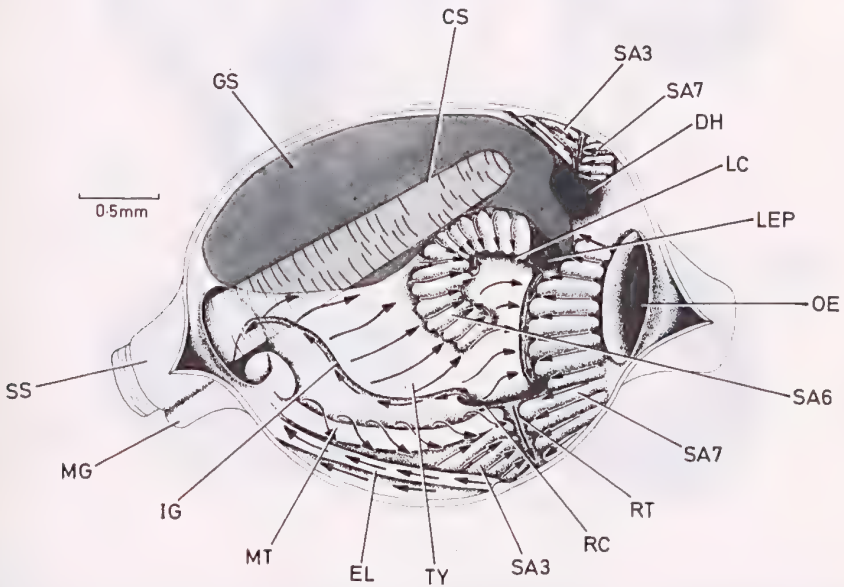


Figure 15. *Fluviolanatus subtorta*. The structure and ciliary currents of the stomach after opening with a horizontal incision along the right wall. (For abbreviations see page 123).

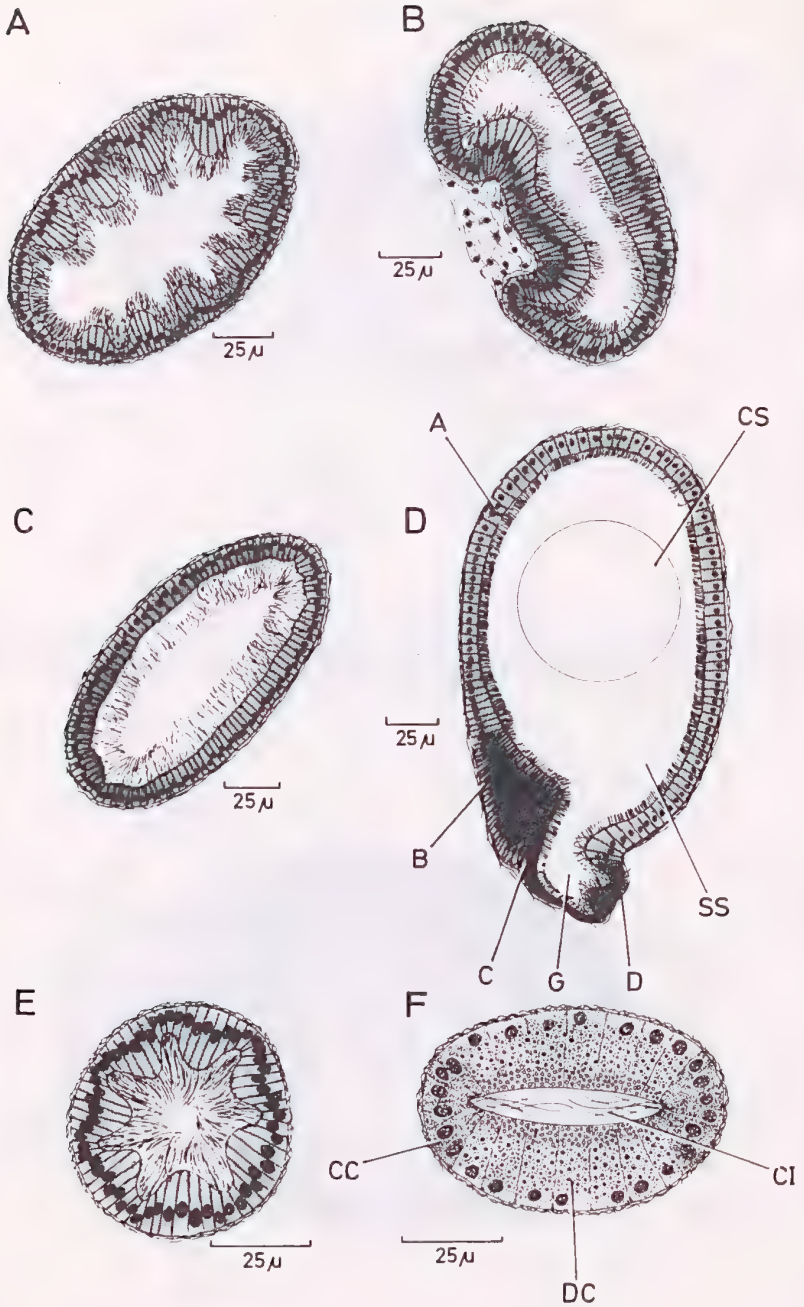


Figure 16. *Fluviolanatus subtorta*. Transverse sections through A, the oesophagus; B, the mid gut; C, the hind gut; D, the style sac; E, the rectum and F, a tubule of the digestive diverticular. (For abbreviations see page 123).

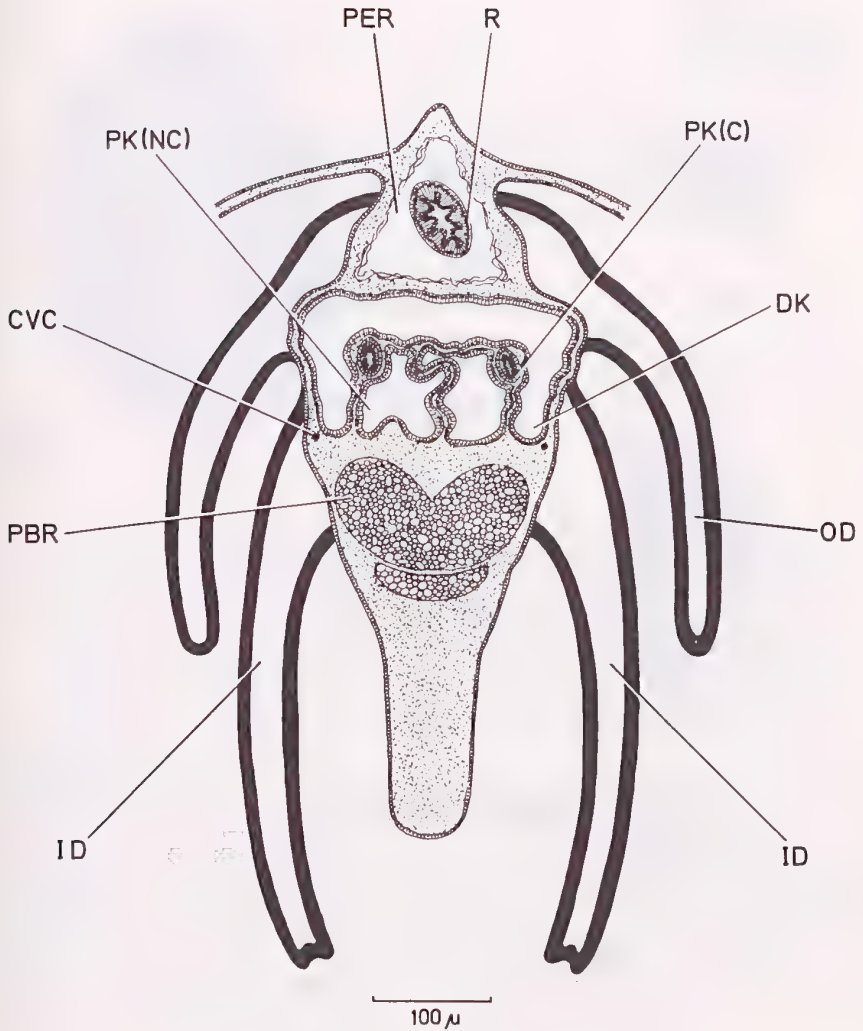


Figure 17. *Fluviolanatus subtorta*. A transverse section through the body in the region of the kidney. (For abbreviations see page 123).

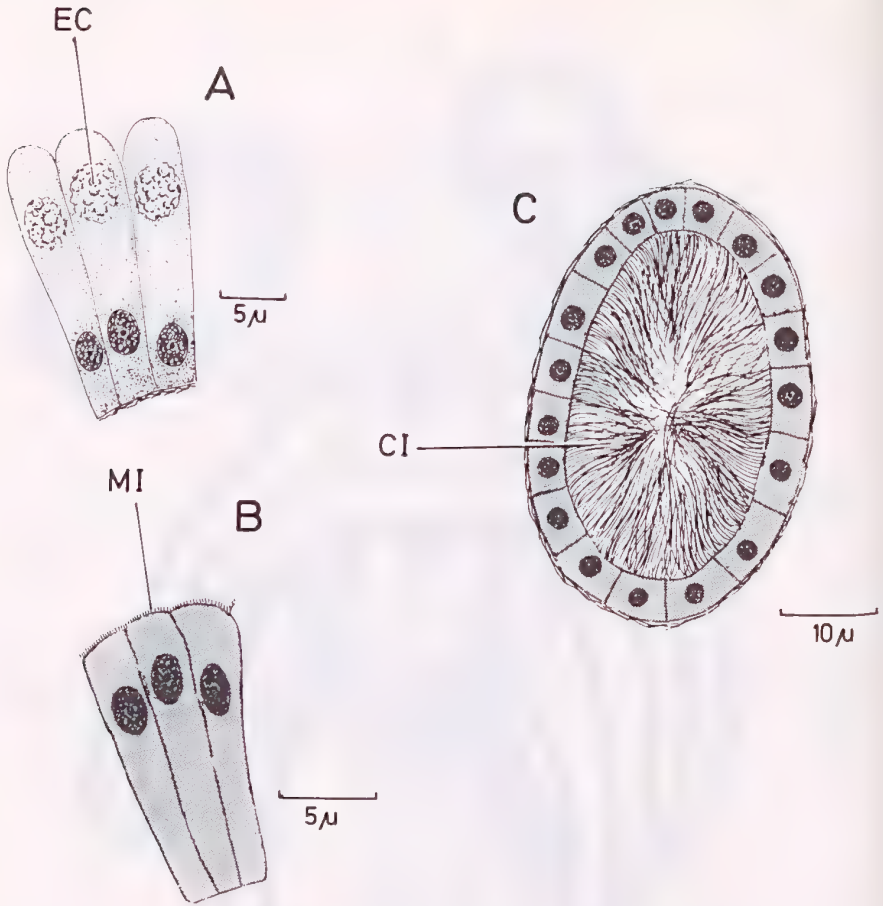


Figure 18. *Fluviolanatus subtorta*. Sections through A, cells of the distal limb of the kidney and B, the non-ciliated region of the proximal limb. C, A transverse section through the ciliated proximal limb of the kidney. (For abbreviations see page 123).